15.—The development of premolar and molar crowns of Antechinus flavipes (Marsupialia, Dasyuridae) and the significance of cusp ontogeny in mammalian teeth

by M. Archer[1]

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Abstract

A series of fourteen transversely sectioned juvenile *Antechinus flavipes* was studied to reveal information about the ontogenetic development of the cheek-teeth. Only three premolar tooth family positions were found. There was no evidence for milk-teeth posterior to the canine. In the upper molars, the first cusp to initiate and calcify was the metacone, followed by the paracone. Stylar cusp D developed and calcified before stylar cusp B. In the lower molars, the protoconid developed and calcified first. The metaconid was generally second. In the M_1 the hypoconid developed and calcified before the paraconid. Reasons are given for believing that ontogeny of tooth cusps does not necessarily indicate phylogeny, and that ontogeny may be at least partly dependent on the size of the cusps of the adult crown.

Introduction

The order in which the cusps develop in molar teeth of mammalia is generally regarded as an indication of the identity of the cusps and in particular of the identity of the paracone and the protoconid. In recent years B. K. B. Berkovitz has shown that in some marsupials (e.g. *Didelphis* and *Setonix)* there must be some doubt as to the general applicability of using ontogeny in this manner.

Here, a study of the developing cusps of the cheek-teeth of *Antechinus flavipes* is made in order to discover the situation in an Australian marsupial which has a structurally primitive dentition.

A series of heads of fourteen juvenile *Antechinus flavipes* of known ages were sectioned transversely. The preparation of specimens used in this study is described by Archer (1974). The sixteen developmental stages examined ranged from the 4 Day Stage (i.e. 4 days postbirth) to the 105 Day Stage and included a 4 Day, 10 Day, 12 Day, 15 Day, "22" Day (actually developmentally younger than the next stage), 21 Day, 28 Day, 32 Day, 36 Day, 40 Day, 44 Day, 51 Day, 59 Day, 60+ Day, 83 Day, and 105 Day Stage. The 83 Day Stage and the 105 Day Stage animals were gross skeletal preparations and are registered in the Western Australian Museum mammal collections as M 8091 and M 8092 respectively.

Cheek-tooth nomenclature follows that of Thomas (1888) bearing in mind that Archer (1974) has established that dP4 is not a milk-tooth and is the first of the dP4-M4 *Zahnreihe*. Basic cusp nomenclature is that used by Bensley (1903) and Simpson (1936), with modifications (Fig. 1) as presented in Archer (1975).

Results

The canine

The upper canine was slightly more advanced in development in any given stage than the lower canine. Enamel knots (Fig. 2) were present in both teeth in the position of the future paracone and protoconid of both crowns. The canines, unlike any of the other cheek-teeth, both had rudimentary uncalcified milk predecessors which were resorbed soon after development.

P1

From its initiation P_1 was in advance of P^1 in development; it also calcified one stage earlier. Both teeth however, were in the same state of development in later stages and in the 60+ Day Stage both had well-formed roots and were nearing eruption. Enamel knots were not observed.

P3

The P_3 was advanced in development over P^3 in all stages observed, although calcification began at approximately the same time in the 40 Day Stage. Enamel knots were not observed.

P4

The P_4 and P^4 developed at about the same time, in the 40 Day Stage. Development was very late and calcification was not observed in the sectioned material.

dP4

DP_4 initiation had begun by the 4 Day Stage. DP^4 was slower in development, initiation occurring in the 10 Day Stage. In later stages however the dP^4 was advanced in development over the dP_4. An enamel knot was observed in both teeth above the area of the presumptive paracone and protoconid, the only cusps that developed on the crowns of these teeth (Fig. 3).

[1] Western Australian Museum, Francis Street, Perth. Present address: Queensland Museum, Fortitude Valley, Queensland 4006.

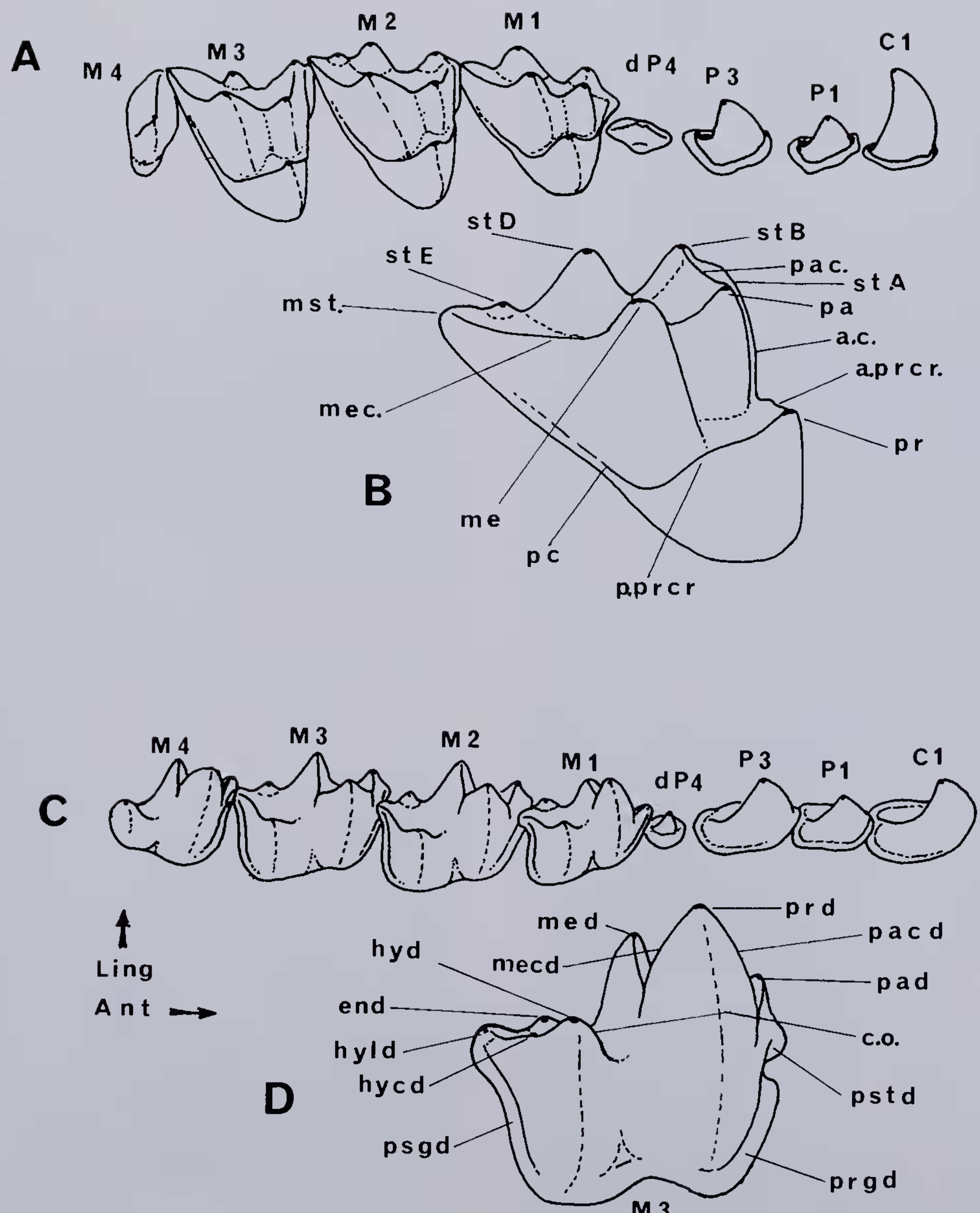

Figure 1.—The morphology of the cheek-teeth. 1A. RC^{1}-M^{4}. 1B. RM^{2}. 1C. RC$_{1}$-M$_{4}$. 1D. RM$_{3}$. Abbreviations: *a.c.*, anterior cingulum; *a. prcr.*, anterior protocrista; c.o., crista obliqua; *end*, entoconid; *hycd*, hypocristid; *hyd*, hypoconid; *hyld*, hypoconulid; *me.*, metacone; *mec.*, metacrista; *mecd*, metacristid; *med*, metaconid; *mst.*, metastylar corner of tooth; *pa.*, paracone; *pac.*, paracrista; *pacd*, paracristid; *pad*, paraconid; *p.c.*, posterior cingulum; *p.prcr.*, postprotocrista; *pr.*, protocone; *prd.*, protoconid; *prgd*, precingulid or anterior cingulum; *psgd*, postcingulid or posterior cingulum; *pstd*, parastylid; *stA*, stylar cusp A; *stB*, stylar cusp B; *stD*, stylar cusp D; *stE*, stylar cusp E.

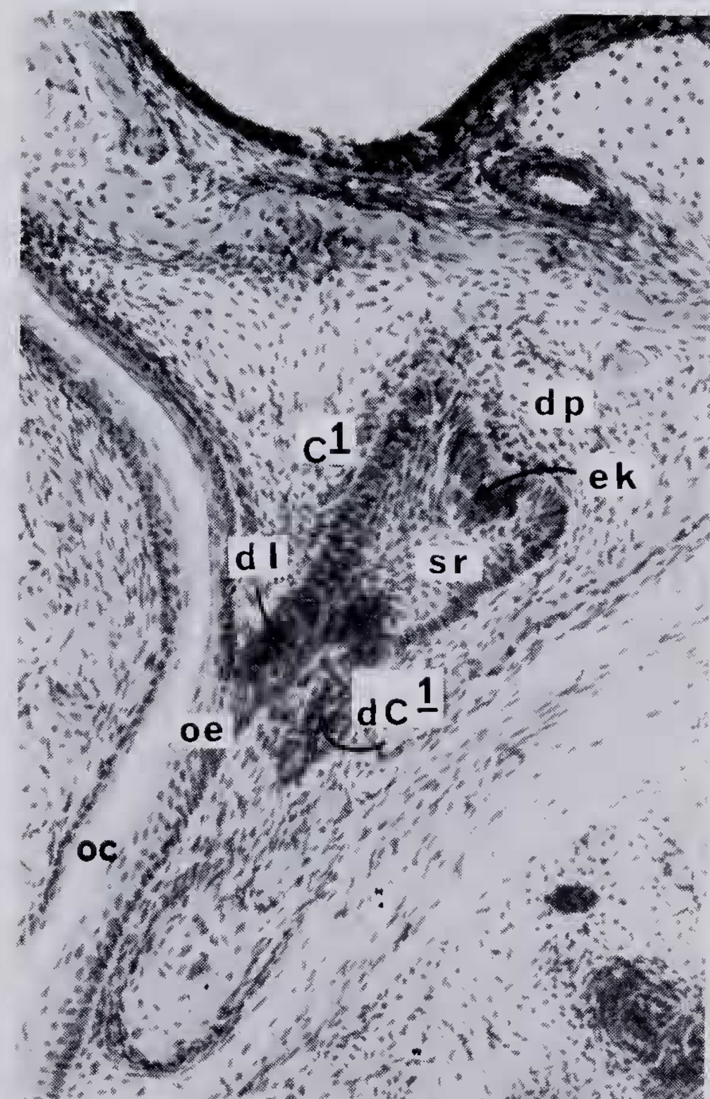

Figure 2.—The upper canine at the 15 Day Stage. Abbreviations; C^1, upper canine; dC^1, rudiment of deciduous canine tooth germ; oe, oral epithelium; dl, dental lamina; sr, stellate reticulum; dp, dental papilla; ek, enamel knot; oc, oral cavity; e, enamel; d dentine x 150.

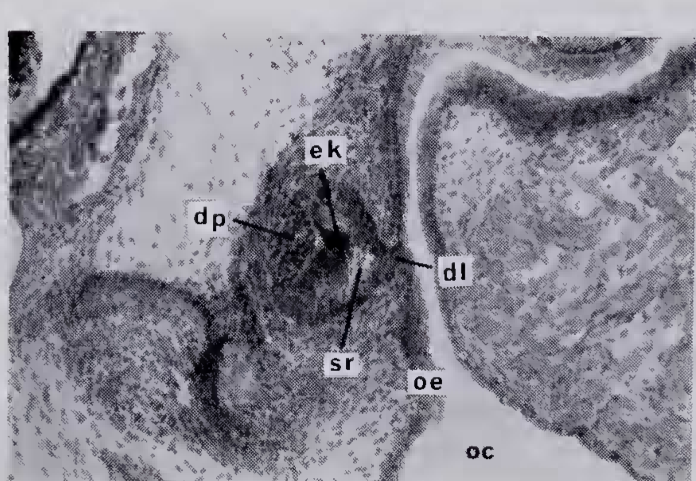

Figure 3.—The upper milk premolar at the 10 Day Stage. Abbreviations as in Fig. 2. x 150.

There were problematical structures associated with the dP^4 and dP_4 in the 60+ Day Stage animal (Fig. 4). These were concentrically laminated epithelial structures developed in the oral epithelium and the enamel epithelium (which at this stage consisted of the inner and outer enamel epithelial layers pressed together) at the tips of the nearly erupting dP4. A similar but smaller structure was observed above the lingual cingulum of the dP^4. These structures may be Pearls of Serres (see Scott & Symons 1961). The dental lamina had completely degenerated from the region of the dP4 in previous stages. These Pearls of Serres were not observed in association with any other teeth but very few teeth were examined at this relatively late stage of development.

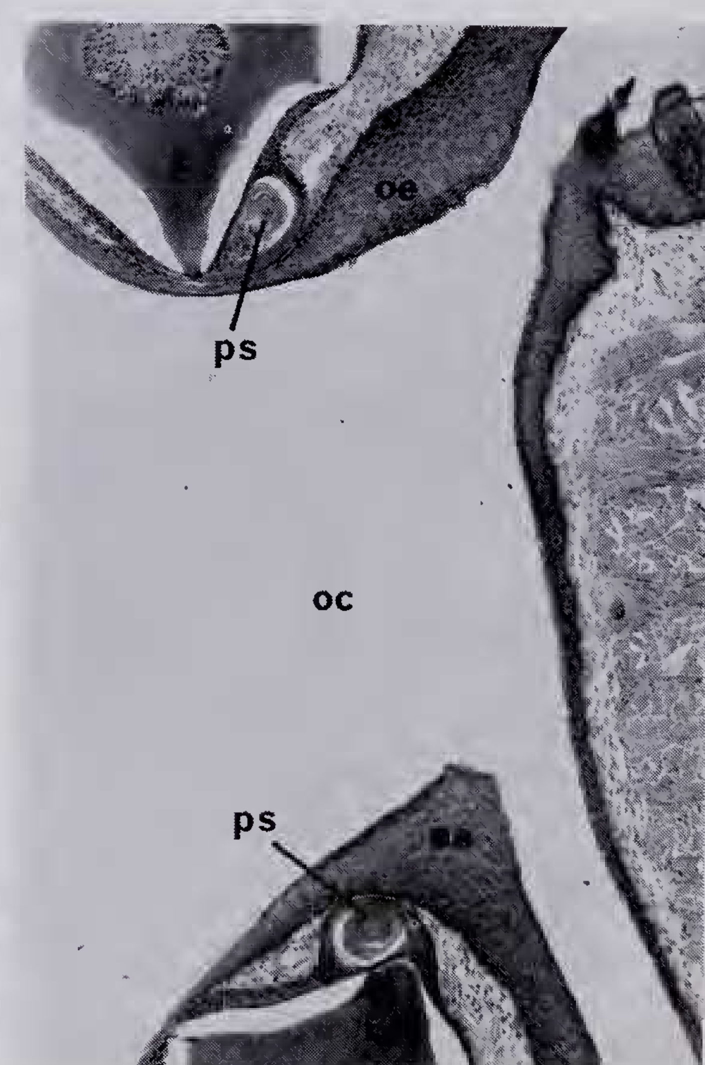

Figure 4.—The upper and lower milk premolar at the 60 + Day Stage. *ps*, tissues resembling Pearls of Serres. Other abbreviations as in Fig. 2 x 75.

M1

M_1 development preceded that of M^1. The first three cusps visible in the 32 Day Stage in M^1 were the metacone, stylar cusp D and the paracone. The metacone was the largest and had begun calcification. Calcification may have just begun at the tip of the paracone in this stage, but clearly had not proceeded as far as it had on the metacone. In the 36 Day Stage stylar cusp D was large but had not begun calcification and the protocone was only beginning to form.

The paracone had clearly become calcified. In the 40 Day Stage stylar cusp D was just beginning calcification (Fig. 5). Stylar cusp B was developed but not calcified. In the 44 Day Stage the protocone was undergoing calcification (Fig. 6). Stylar cusps B and A did not undergo calcification until the 51 Day Stage.

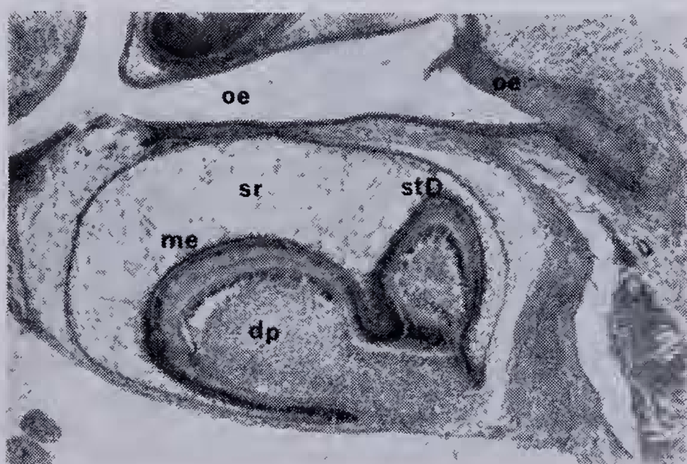

Figure 5.—The upper first molar, section through the metacone and stylar cusp D, at the 40 Day Stage. Both cusps are undergoing calcification. At this stage only the metacone, stylar cusp D and the paracone were calcified. *me,* metacone; *st.D,* stylar cusp D. Other abbreviations as in Fig. 2 x 75.

Figure 6.—The upper first molar, section through the protocone, paracone and stylar cusp A at the 44 Day Stage. Only the paracone is shown calcified but the beginning calcification of the protocone is apparent in sections posterior to the section shown. At this stage the metacone and stylar cusp D are also calcified. *pr,* protocone; *pa,* paracone; *st.A,* stylar cusp A. Other abbreviations as in Fig. 2. x 75.

In M^1 the protoconid was the first cusp to become visible in the 15 Day Stage as well as to calcify in the 21 Day Stage. The hypoconid and metaconid were distinguishable but uncalcified in the 36 Day Stage. All of these cusps had begun calcification by the 40 Day Stage but the hypoconid was the least developed. The entoconid may have been distinguishable in the 44 Day Stage. By the 51 Day Stage the paraconid had begun calcification. The entoconid and hypoconulid may have just begun calcification.

M2

In M^2 the metacone was distinguishable in the 40 Day Stage. By the 44 Day Stage the paracone, protocone, stylar cusp D and possibly stylar cusp B had also appeared but only the metacone had clearly become calcified (Fig. 7a). The paracone may have just begun calcification (Fig. 7b). The paracone had clearly begun calcification by the 51 Day Stage and all major cusps had become calcified by the 59 Day Stage.

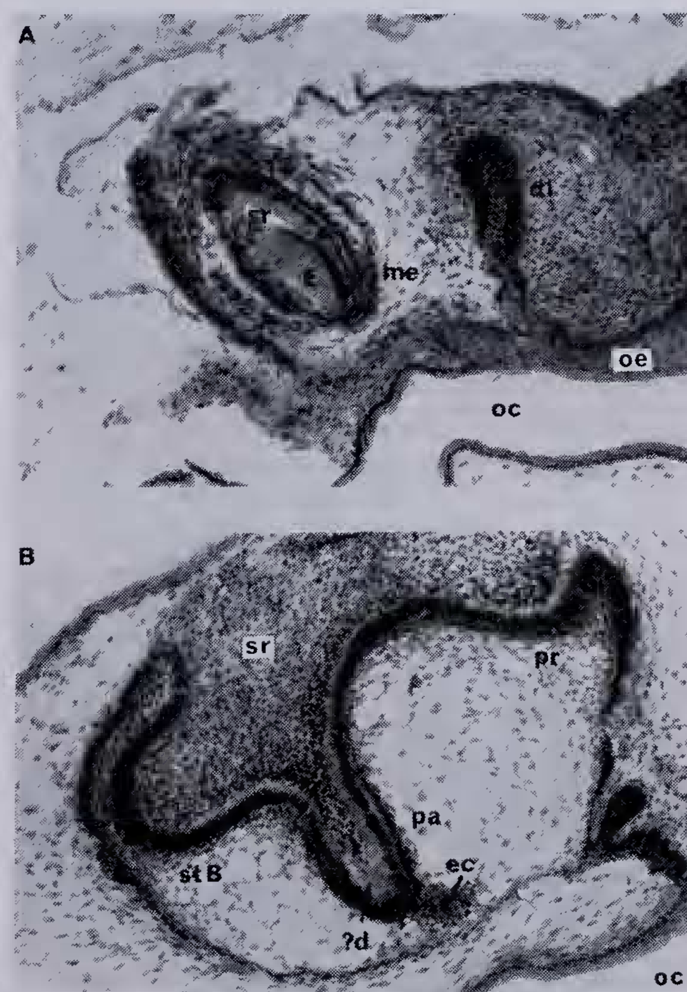

Figure 7.—The upper second molar at the 44 Day Stage. 7A. Section through the well-calcified metacone showing enamel as well as dentine, and the posteriorly extended dental lamina. 7B. Section through the protocone, paracone and stylar cusp B showing the slight (if any) calcification of the paracone. There appears to be an enamel cord above the paracone tip. *ec,* enamel cord. Other abbreviations as in Figs. 2, 5 and 6. x 150.

In M_2 in the 36 Day Stage, the protoconid, metaconid, paraconid and possibly the hypoconid were present but only the protoconid had begun calcification. In the next stage the metaconid had calcified. The entoconid appears to be distinguishable by the 44 Day Stage. The paraconid did not begin calcification until the 51 Day Stage. The entoconid was calcified by the 59 Day Stage.

M3

The metacone of M^3 was first distinguishable in the 59 Day Stage. It was uncalcified. An enamel cord was observed over the tip of the cusp (Fig. 8). By the 60+ Day Stage, the paracone, metacone and protocone were distinct but only the first two had undergone calcification.

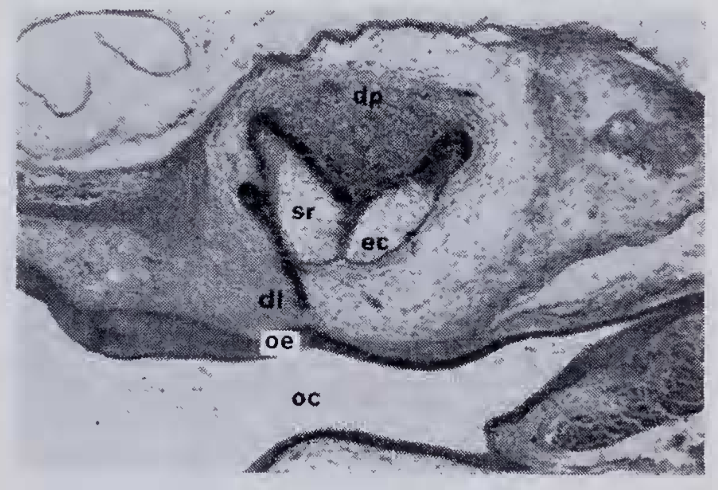

Figure 8.—The upper third molar at the 59 Day Stage showing an enamel cord over the tip of the metacone. Abbreviations as in Fig. 7. x 75.

In M_3 the metaconid and protoconid were present in the 44 Day Stage but only the latter was calcified. The paraconid was distinguishable in the following stage. By the 59 Day Stage all cusps were present and all were calcified except the entoconid and hypoconulid. By the 60+ Day Stage the hypoconulid had begun calcification.

M4

The M^4 in the 60+ Day Stage was merely a swelling of the dental lamina. The M_4 on the other hand had all three trigonid cusps formed and calcified in the 60+ Day Stage.

Table 1 summarizes the data presented above.

Discussion

Cusp formation and homology

In 1874 Cope proposed that the complex therian molar had developed through addition of cusps peripheral to a single cusp of a primitive tooth. This basic premise was in contrast to that of others such as Bolk (1922) in which the therian molar was seen as a result of fusion of adjacent single-cusped primitive teeth. Cope's premise has generally been accepted (e.g. see Gregory 1934, Butler 1941, Crompton 1971). However, there has been disagreement about which cusp on the therian molar is the primitive cusp. Osborn (1888) believes it is the lingual cusp or protocone of the upper molar and the antero-buccal cusp or protoconid of the lower molar. This view has been accepted by many later authors (e.g. Gregory 1934, Simpson 1936). Winge (1941) however believes that the variably present external stylar cusps of the upper molars and the three lingual cusps, the paraconid, metaconid and entoconid of the lower molars are the oldest cusps and therefore the central stylar cusp and the metaconid represent the ancestral primitive cusps. Gidley (1906) suggests that the paracone of the upper molars and the protoconid of the lower molars were the first ancestral cusps. Gregory's view has been supported by Wortman (1902) and Butler (1937) who argue that on the basis of observations of upper premolars that when these teeth become progressively molarized posteriorly along the tooth row through evolution, they often produce secondary cusps serially homologous with the protocone and metacone, suggesting that the ancestral cusp is the paracone in upper molars as well as premolars. Embryological evidence of Röse (1892a), Taeker (1892), Woodward (1896), Kupfer (1935), Marshall & Butler (1966), and Berkovitz (1968) indicates that in marsupials and eutherians the paracone and protoconid develop first ontogenetically and Butler (1956) concludes that this supports the view that these cusps are the ancestral molar cusps. However, Röse (1892b) and Berkovitz (1967a) have observed that in some molariform marsupial teeth examined, the metacone developed first.

The results of Röse (1892b) and Berkovitz (1967a) appear to cast doubt on the concept that position in the ontogenetic sequence of cusp development can indicate the primary cusps. It is also possible, but not likely, that the cusp called a metacone in these marsupials is homologous with the paracone of other marsupials (e.g. *Trichosurus* and *Setonix*) and mammals in general. It is also possible, as Butler (1956) suggests, that Röse (1892b) may not have used the same criteria as other authors to establish the state of development of a cusp but this is not likely because Berkovitz (1967a) has confirmed Röse's (1892b) observations in a specimen of the same genus (*Didelphis*).

Upper molars

In the M^{1-2} of *Antechinus flavipes* examined in the present study it is apparent that the metacone precedes all the other cusps in development and calcification. This may also be the situation in M^{3-4}. The paracone is the next cusp to form and calcify, followed by the protocone. This developmental sequence is unlike any other reported except for that of *Didelphis* (Röse 1892b, Berkovitz 1967a). It also appears to contrast with the findings of Woodward (1896) who after examining one specimen of *Antechinus* sp. states (p. 284) that "The paracone above and the protoconid below develop before any of the other molar cusps". However, some doubt about Woodward's conclusion must stem from the fact that he examined only one specimen and, as indicated by the present study, this may not be sufficient. In view of the results reported in this paper there appears to be reason for believing that the paracone may not always pre-

Table 1

Day Stage post-birth in which initiation (i) and calcification (c) of molar cusps was observed.

UPPER

	M^1		M^2		M^3		M^4	
	i	c	i	c	i	c	i	c
protocone	36	44	44	59	60+	83	?	?105*
paracone	32*	?32*	44	51	60+	60*+	?	105*
metacone	32*	32*	40*	44*	59*	60*+	....	....
stylar cusp A	51	51	59	59	?	105	....	....
stylar cusp B	40	51	?44	59	?	83	?	?105*
stylar cusp D	32*	40	44	59	?	83	....	....

LOWER

	m_1		m_2		m_3		m_4	
	i	c	i	c	i	c	i	c
protoconid	15*	21*	36*	36*	44*	44*	60*+	60*+
paraconid	51	51	36*	51	51	59	60*+	60*+
metaconid	36	40	36*	40	44*	59	60*+	60*+
hypoconid	36	40	?36*	?44	59	59	?	83
entoconid	?44	51	?44	59	59	83	....	....
hypoconulid	51	51	?	?	59	60+	....	....

* first occurrence.

cede other cusps in development. Since other marsupials examined, e.g. *Setonix* (Berkovitz 1967b) and *Trichosurus* (Berkovitz 1968) demonstrate that the paracone develops first, this could be interpreted as suggesting the marsupials are polyphyletic with regard to molar formation. An alternative explanation is that the order of cusp development may not be an invariable indicator of the order of cusp evolution of the marsupials in which the metacone develops first. Both *Didelphis* and *Antechinus* differ from other marsupials examined ontogenetically by having a metacone which is the largest cusp on the crown and certainly larger than the paracone (Fig. 1). In *Setonix, Trichosurus* and most other phalangeroids, the metacone and paracone are subequal. In most other mammal species previously examined the morphology of the adult crowns (for examples see Butler 1956) shows that the paracone is subequal to or even larger than the metacone. Butler (1967) concludes, from research into the relative growth of the first upper permanent molar in *Homo*, that the antero-buccal areas (i.e. the area of the paracone) of the crown develop before the postero-lingual areas and interprets this as indicating the probable order of cusp origin in phylogeny. However, Butler (1956) had previously suggested (relying on the research of Canalis 1886 and others) that cusp initiation is the result of a cessation of mitoses at a point on the inner enamel epithelium, the remainder of the crown cusps being subsequently developed in a similar way, while active mitosis, which continues to occur in areas between the cusps, results in enamel deposition in the valleys. Accordingly the cusp destined to be the tallest on the completed crown would presumably be the first to be initiated, and the cusp destined to be the lowest on the crown would be the last to become initiated. Butler's (1956) suggestion would therefore support the hypothesis that the phylogenetic sequence of development of the cusps in *Didelphis* and *Antechinus* may be modified in ontogeny by the great height of the definitive metacone.

It is also possible that the rate of development of the cusps of a crown are not identical. If so, a primary cusp could develop first, but by its surrounding valley developing more slowly than that of a secondary cusp, appear to have developed after the secondary cusp. For example as noted above, in the M^1 of *Antechinus flavipes,* at the 32 Day Stage, the metacone was clearly calcified and better-developed than the paracone. Were this the only stage available, it would be open to interpretation that the paracone had been initiated first, but been slower in development than the metacone. That this is not the case (at least in M^2) is demonstrated in this series by the fact that the metacone was first distinguishable in the 40 Day Stage, while the paracone was not distinguishable until the 44 Day Stage.

The development of the stylar cusps reveals a similar problem in interpreting phylogeny from ontogenetic sequence. In the M^1 stylar cusp D appears and calcifies prior to stylar cusp B. Many Mesozoic fossil therians have well developed stylar cusps (e.g. *Pappotherium*), but the basis for determining the homology of these cusps is dubious. Slaughter (1965), Clemens (1968 and 1971), Kermack, Kermack, & Mussett (1968), and others however all recognize the antiquity of stylar cusp B, often referred to as the stylocone. It is identified topographically as the buccal cusp generally connected by a crest to the paracone (Fig. 1). This cusp is present in *Antechinus flavipes*. Stylar cusp D is posterior to but much larger than stylar cusp B. The relatively early development and calcification of stylar cusp D compared with stylar cusp B in *A. flavipes* appears to be a situation directly comparable with that of the relatively early development and calcification of the metacone compared with the paracone.

Lower molars

In the lower molars of the series, the protoconid invariably developed and calcified first. The metaconid was generally second. In the M_1 the hypoconid developed and calcified before the paraconid. In $M_{2\text{-}4}$ the paraconid seems to have developed and calcified in advance of the hypoconid. The hypoconulid and entoconid were usually the last to develop and calcify. In the M_1 however the entoconid developed before the paraconid.

As pointed out by Butler (1956) and subsequently shown by Berkovitz (1968), the protoconid of mammals appears to develop and calcify first (a possible exception in *Setonix* is described by Berkovitz 1967b). No exception would have been expected for *Antechinus* because in that form the protoconid is the largest cusp of each molar (Fig. 1). Röse (1892b) and Berkovitz (1967a, 1968) demonstrate that the metaconid in *Didelphis* and *Trichosurus* is the second cusp to develop in the lower molars, as in *Antechinus*. Butler (1956) reviews other studies (e.g. Woodward 1896, on *Setifer*) which show that in some mammals the paraconid is the second cusp to develop. The paraconid is vestigial or absent in *Trichosurus*. However in *Didelphis* (Röse 1892b) the paraconid develops late, as in the M_1 of *Antechinus*. The relative size of the paraconid in $M_{1\text{-}4}$ of *Antechinus* may account for the differences in the rate of development between M_1 and $M_{2\text{-}4}$. In M_1 the paraconid is very reduced in contrast to its condition in $M_{2\text{-}4}$. As noted above, it would be expected to develop later in M_1. Butler (1956, p. 51) comments in reference to the varying time of development of the paraconid in mammals that "This variation in the time of appearance of the paraconid is in accordance with its relative size . . . ".

Berkovitz (1967b) describes cusp formation in the macropodid marsupial *Setonix*. He shows that although the cusp he calls the protoconid of the M_1 develops first, a cusp he identifies as the metaconid on the dP_4 develops first. To account for this he concludes that the larger size of the metaconid of the dP_4 is the reason it develops before the protoconid.

Conclusion

The results reported in this study for the lower as well as upper molars of *Antechinus* support the suggestion of Berkovitz (1967b) that the relative size of cusps is at least as important as phylogeny in determining the sequence of development during ontogeny. It may be that if the cusps are equal in height, ontogeny can reveal phylogeny. Since, however, in most living eutherians in which the paracone and metacone are unequal the paracone is larger, belief that early development of the paracone in these forms supports the contention that this cusp is the ancestral cusp is warranted but does not show conclusively that this is so because the reason for prior development may be cusp size alone. *Didelphis* and *Antechinus* represent a marsupial lineage in which there was selection for a larger metacone. This innovation probably imposed a practical need in these forms to have the larger metacone develop in advance of the smaller paracone.

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